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The soil fauna of beech forests: comparison between a mull and a moder soil

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With 3 figures

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1. Introduction

Prevailing humus types of Central European deciduous forests are mull and moder or intermediate forms (KÜHNELT, 1961; WALLWORK, 1976; PETERSEN & LUXTON, 1982). In moder soil the current litter (L) lies over a layer of partly decomposed material (O_f – the fermentation layer), in which the degree of decomposition increases with depth. The O_f layer grades into a thin lower horizon, the humus horizon (O_h), of well-decomposed organic material, visibly unrecognizable as to plant origin. Normally the O_h horizon shows a rather abrupt transition to the underlying mineral soil horizon (A), usually with some kind of mechanical mixing of organic and mineral particles (A_h horizon).

In the mull soil there is no distinct L-O_f-O_h stratification. A litter layer (L) may be present. However, the current litter may be essentially absent towards the end of the growing season, just before major leaf fall. Individual pieces of partially decomposed organic matter may constitute an ill-defined O_f layer. An O_h horizon is not present. The thin organic layer (O) is not clearly separated from the soil. The uppermost soil horizon (A_h) is an intimate mixture of well-humified organic matter and mineral soil.

The formation of either moder or mull depends on the type of soil parent material, abiotic soil factors, macroclimate and tree species.

The standing crop of soil organic matter is lower in mull than in moder soils under equilibrium conditions with the same litter input. In mull *p*H values, degrees of base saturation and Ca or Mg availability are higher; the structure of humus-rich mineral topsoil is more diverse; crumb formation is characteristic; and C:N ratio is low, with a value below 15. Mull soils normally bear a diverse herb layer. More details are given in WALLWORK (1976) and SWIFT *et al.* (1979).

It is well established that the composition of the soil biota is related to the humus type. Acid soils are not favourable for bacterial populations. Apart from direct effects of acidity on bacteria, the absence of macroorganisms such as earthworms appears to be a negative factor (SPURR & BARNES, 1980). Under conditions unfavourable to bacterial growth, fungi are better able to survive, grow, and become dominant. Some results of the numerous studies on the soil fauna (cf. PETERSEN & LUXTON, 1982) are: mull soils favour the macrofauna and are characterized by high zoomass; moder and mor soils contain a lower zoomass and are dominated by the mesofauna.

A disadvantage of the soil fauna surveys summarized in PETERSEN & LUXTON (1982) is that the studied forests belong to different geographic regions. Forest ecosystem analyses in the southern part of Lower Saxony (Germany) gave the opportunity to compare the animal component of two beech forests, about 55 km apart, that belong to the same geographic and climatic region: a beech wood on limestone (Göttinger Wald) (SCHAEFER 1989a, 1989b, 1989c, 1989d, 1989e) and a beech wood on acid soil (Solling) (FUNKE, 1973; ELLENBERG *et al.*, 1986).

In the following survey we give a general account of the animal fauna in the two beech forests, focusing on species spectrum, population density and biomass of invertebrates. Base data of the

fauna of the two forests allow to test the following hypotheses concerning structural and functional characteristics of the soil animal community:

(1) Mull, with its base-rich conditions, is dominated by macrofauna, whereas moder, as an acidic milieu, is dominated by mesofauna.
(2) Because mull soils constitute a less extreme environment in comparison to moder soils, species diversity indices (richness and evenness) are higher in mull soils.
(3) In moder soils, which are clearly stratified, animal life is concentrated in the organic horizons and a thin upper layer of the mineral soil; in mull soil the fauna penetrates to deeper soil horizons.
(4) In the mull forest, with its less continuous supply of recources, more sharply defined phenophases occur, whereas more continuous phenological events characterize moder soil conditions.
(5) In the mull forest, with its diverse herb layer, food utilization patterns are spatially and temporally more diverse; moder conditions lead to more uniform patterns of food intake.
(6) Animals of the mull and moder forest are of comparable importance in energy flow. However, the high proportion of primary decomposers under mull conditions is responsible for higher decomposition rates in this forest type.
(7) Because of the presence of high macrofauna biomass, mineralization processes are more continuous in the mull soil. Hence, mineral cycling is more susceptable to stress in moder soils than under mull humus conditions.

Some deficiencies of our approach should not be concealed. The samples have been collected by a diversity of persons and often do not relate to the same year. There are considerable gaps in the sampling program, mainly involving the microfauna in the moder forest.

2. Study sites and methods

2.1. Beech forest Göttinger Wald ("GÖ")

The beech forest Göttinger Wald (abbreviated as "GÖ" in the following paragraphs) is situated in southern Lower Saxony (West Germany) on a plateau of Muschelkalk with an elevation of about 420 m above sea level. The beech forest about 8 km east of Göttingen is approximately 100–115 years old and has a rather uniform canopy layer consisting almost exclusively of beech (*Fagus sylvatica* L.) trees, which form a dense crown layer. Some trees of other species, mostly ash (*Fraxinus excelsior* L.), and maple (*Acer platanoides* L.), and more rarely *Acer pseudoplatanus* L., *Quercus robur* L., *Q. petraea* (MATT.) LIEBL and *Ulmus scabra* MILL., are interspersed. A shrub layer is not developed, though in gaps there is a higher growth of young *F. excelsior* trees. The herb layer is, with few exceptions, dense and diverse. Dominant spring geophytes are *Allium ursinum L.* and *Anemone nemorosa* L.; additional dominant herbs are *Asarum europaeum* L., *Hordelymus europaeus* (L.) JESS., *Galium odoratum* (L.) SCOP., *Lamiastrum galeobdolon* (L.) NATH., *Mercurialis perennis* L., *Oxalis acetosella* L. and *Primula elatior* (L.) HILL. The forest belongs to the Melico-Fagetum hordelymetosum (DIERSCHKE & SONG, 1982; consult for further details). The soil, which is shallow and belongs to the soil series on carbonate rocks, consists of "terra-fusca-rendzina" (about 50%), rendzina (about 26%), terra fusca (about 14%), and some other modifications containing brown earth (MEIWES & BEESE, 1988). The organic layer contained leaf material of a mean annual mass of 550 g dry mass $\cdot m^{-2}$; annual canopy leaf litter fall amounted to 348 g dry mass $\cdot m^{-2}$ in 1982 and 272 g dry mass $\cdot mg^{-2}$ in 1983. The *p*H ranges from 6.8 to 4.3 with a mean value of about 5.8. Cation exchange capacity is high. Mean annual temperature is about 7 °C, mean annual precipitation is around 700 mm (VAN EIMERN & EHRHARDT, pers. comm). Further details are given by SCHAEFER (1989a, 1990).

2.2. Solling Beech forest ("SO")

This forest (abbreviation: "SO") is located on the plateau of the High Solling, a mountain range of medium altitude (500 m above sea level) about 55 km northwest of Göttingen. It is a pure beech *(Fagus sylvatica)* stand without a shrub and herb layer, and can be classified as a Luzulo-Fagetum. Parent material of this acidophilous forest is a loess creeping earth of 40–60 cm thickness above a paraautochthonic creeping earth consisting of loamy weathered Buntsandsein material. The unweathered Buntsandstein of Triassic age begins at depths of about 100 cm.

Hence the soil belongs to the series on carbonate-free silicate rocks: it is an acid brown earth with a moder humus form. The mass of organic layer on the soil increased from 2,960 $g \cdot m^{-2}$ in the year 1966 to 4,460 g dry mass $\cdot m^{-2}$ in 1979; annual canopy leaf litter fall had a mean value of 290 g dry mass $\cdot m^{-2}$ for the period from 1967 to 1976. Values of *p*H range from about 3 to 4. Cation exchange capacity is low. Mean annual precipitation is 1,063 mm. Further details are given in ELLENBERG *et al.* (1986).

2.3. Sampling procedure and determination of biomass

The fauna has been sampled on two study areas with an array of different methods (*cf.* ELLENBERG *et al.*, 1986; SCHAEFER, 1990): extraction of soil and litter samples with a KEMPSON bowl extractor for the macrofauna (diameter of the soils cores 21.5 cm); extraction with a MACFAYDEN high gradient canister apparatus (modified by SCHAUERMANN) for the mesofauna (diameter of the cores 5.5 cm); extraction with O'CONNOR wet extractor for the semiaquatic fauna (diameter of the cores 3.2 cm); hand-sorting in the case of earthworms (with additional application of a 0.75% solution of formaldehyde) and gastropods, plot size was 25 cm × 25 cm; sampling with pitfall traps, ground photo-eclectors (covering 1 m^2) and arboreal photo-eclectors (*cf.* FUNKE, 1971). Samples were taken in monthly intervals, in most cases 12 parallels per date and separated into different layers: in GÖ litter, mineral soil layers −3 cm, −6 cm, −9 cm, −12 cm; in SO L + O_f horizon, O_h + A_h horizon, mineral soil layers −5 cm, −10 cm, −15 cm. Most sampling data of the SO soils relate to the years 1972 to 1975; in GÖ the base sampling period ranged from 1981 to 1982.

In most cases animal biomasses were determined as "ash-free dry mass" (dry mass = xeromass) by weighing specimens that were killed by freezing and then dried for 48 h at 60 °C under vacuum conditions. For the arthropods lengh- and/or width-to-mass regressions were used to calculate the biomass of preserved specimens in the samples.

2.4. Mathematical treatment of the data

Instead of calculating diversity indices, rank-abundance patters are presented graphically.

Mean depth for soil animal taxa was calculated according to the formula of USHER (1970)

$$M_i = \frac{\sum_{i}^{k} d_i \cdot n_i}{N}$$

(k = number of strata, d_i = mean depth of stratum i, n_i = number of animals in stratum i, $N = \sum n_i$). Reference line for the analysis of depth distribution is the boundary between O_h and A_h layer. For the calculation of mean depth the value zero is assigned to this borderline. The proportions of a population in the organic layers are included in the calculation with a positive sign, the parts of a population in the mineral layers with a negative sign. In GÖ, L and O_f have a mean value of 3 cm; the soil layers were counted with the depths 0−3, 3−6, 6−9, 9−12 cm, as indicated above. In SO, mean values of L are 2.8 cm, of O_f 1.7 cm, of O_h 1.2 cm, of A_{he} 3.3 cm (according to BABEL in ELLENBERG *et al.*, 1986).

3. Results

3.1. Composition of the fauna: species, abundance, biomass

Data base for the SO soil fauna is the monograph by ELLENBERG *et al.* (1986). A recent analysis of the SO oribatid fauna is given by HEILIGENSTADT (1988). Sources for ecological data about the mull soil fauna in GÖ are, in the sequence given by table 1: Protozoa (MEISTERFELD, 1989), Nematoda (BÜTTNER, 1988), Turbellaria, Rotatoria, Tardigrada, Harpacticoida (BÜTTNER, 1983), Enchytraeidae (MELLIN, 1988), Uropodina (SCHULZ, 1986), Diplura, Protura, Collembola (WOLTERS, 1983, 1985), Gamasina (SCHULZ, 1986), Gastropoda (CORSMANN, 1981), Lumbricidae (JUDAS, 1989; JUDAS et al., 1989), Isopoda (STRÜVE-KUSENBERG, 1987), Diplopoda (SPRENGEL, 1986), Elateridae (MORITZ, 1986), Diptera (HÖVEMEYER 1984, 1985), Araneida, Pseudoscorpionida (STIPPICH, 1986), Opilionida (BACHMANN & SCHAEFER, 1983), Chilopoda (POSER, 1984), Carabidae (MARTIUS, 1986), Staphylinidae (SCHAEFER, 1983). Unpublished results are given for groups not mentioned in this enumeration (*cf.* SCHAEFER, 1989e).

Table 1. Synopsis of species richness (S), mean annual population density (N, ind · m^{-2}) and mean annual biomass (B, mg dry mass · m^{-2}) in the beech forests Göttinger Wald (with mull soil) and Solling (with moder soil).

Animal Group	Göttinger Wald			Solling		
	S	N	B	S	N	B
Microfauna						
Flagellata	–	2.7×10^9	54	–	–	–
Amoebina	–	3.5×10^9	1133	–	–	–
Testacea	65	84×10^6	343	51	57×10^6	256
Turbellaria	3	859	8	3	1882	4
Nematoda	65	732000	146	–	–	–
Tardigrada	4	4207	4	–	41[a])	9[a])
Harpacticoida	–	3873	2	1	3300[a])	0.6[a])
Saprophagous and microphytophagous mesofauna						
Enchytraeidae	36	22300	600	15	108000	1640
Cryptostigmata	61	25900	180	72	101810	195
Uropodina	11	3390	26	4	1525	–
Symphyla	2	57	–	1	–	–
Diplura	–	161	–	> 1	277	–
Protura	–	2481	–	> 1	278	–
Collembola	48	37835	153	> 11	63000	246
Zoophagous mesofauna						
Gamasina	67	2620	45	13	10800	397
Saprophagous macrofauna						
Gastropoda	30	120	430	4	0	0
Lumbricidae	11	205	10700	4	19	168
Isopoda	6	286	93	0	0	0
Diplopoda	6	55	618	1	0	0
Elateridae larvae	11	37	104	4	332	706
Diptera larvae	37[b]) (>245 spp.)	2843	161	40[b])	7415	628
Zoophagous macrofauna						
Araneida	102	140	47	93	462	173
Pseudoscorpionida	3	35	16	2	89	10
Opilionida	8	19	11	4	20[a])	6[a])
Chilopoda	10	187	265	7	74	155
Carabidae	24	5	144	26	7	93
Staphylinidae	85	103	76	117	314	180

[a]) single measurement; [b]) families.
– = not studied; 0 = not present. Data from different sources (see text). Some minor groups are omitted. For further explanation see text.

Some general results emerge from the synopsis of the more important animal groups in the two forests (table 1). Total soil zoomass amounts to about 15 g dry mass · m^{-2} in the mull soil and about 5 g dry mass · m^{-2} in the moder soil. This difference is mainly due to the predominance of earthworms and, to a lesser degree, of saprophagous macroarthropods in the mull forest. Mainly microphytophagous mesofauna groups dominate in the moder environment. Zoophagous macroarthropods occur in comparable numbers in both forest types. In the following section some more detailed comments on dominant species, abundance and biomass relations of important edaphic groups are given.

Microfauna: Only the Thecamoeba were studied in detail in both forests, although values for SO appear to be preliminary (MEISTERFELD, 1980). Mean population densities and biomass

values of the testate amoebae were comparable in SO and GÖ. The mull forest is characterized by high population densities of Flagellata and naked amoebae (MEISTERFELD, 1989). The latter group – consisting mainly of bacterial feeders – has high biomass values.

Among the other microfaunal groups the Nematoda are clearly the most abundant (BÜTTNER, 1988).

Saprophagous and microphytophagous mesofauna: Enchytraeidae are more important in SO: the dominant species is *Mesenchytraeus glandulosus* (LEVINSEN, 1884), which accounts for almost one third of the enchytraeid biomass (ELLENBERG *et al.*, 1986). In GÖ MELLIN (1988) found 36 enchytraeid species, with a more even distribution of number of individuals among species. *Achaeta* spp., *Fridericia* spp. *Mesenchytraeus armatus* (LEVINSEN, 1884) and *Stercutus niveus* (MICHAELSEN, 1888) are dominant, measured as biomass. The moder population has a significantly lower mean body mass (0.015 mg dry mass) as compared to GÖ (0.027 mg dry mass).

Oribatid abundance is significantly higher in the moder than in the mull soil. However, biomass does not distinctly surpass values for the mull soil (mean body mass of mites in SO 0.002 mg, in GÖ 0.007 mg dry mass). In GÖ the oribatids *Steganacarus magnus* (NICOLET, 1855), *S. striculus* (C. L. KOCH, 1836) and *Nothrus palustris* C. L. KOCH, 1840, dominated in biomass. In SO *Platynothrus peltifer* (C. L. KOCH, 1839), *Nothrus silvestris* NICOLET, 1855, *Nanhermannia coronata* BERLESE, 1913, and *Chamobates voigtsi* (OUDEMANS, 1902) constituted over 50% of adult zoomass (HEILIGENSTADT, 1988).

In GÖ mean annual population density and biomass of Collembola are about half of the corresponding SO numbers. Thus mean body mass is almost the same in both habitats (0.004 mg dry mass). In GÖ several collembolan species dominate (measured in biomass): *Tomocerus flavescens* (TULLBERG, 1871), *Lepidocyrtus lignorum* (FABRICIUS, 1781), *Folsomia quadrioculata* (TULLBERG, 1871), *Isotomiella minor* (SCHÄFER, 1869), *Hypogastrura denticulata* (BAGNALL, 1941) [WOLTERS, 1983].

Zoophagus mesofauna: Gamasids as mesofaunal predators occur in higher numbers in SO; additionally, gamasid mean body mass (0.368 mg dry mass) is distinctly higher than that of GÖ (0.172 mg dry mass). Dominant gamasid mites in GÖ are *Pergamasus lapponicus* TRÄGÅRDH, 1912, and *Veigaia nemorensis* C. L. KOCH, 1893 [SCHULZ, 1986]; the latter species has also high population density values in SO (SCHULZ, pers. comm.).

Saprophagous macrofauna: In comparison to the moder milieu, the GÖ mull soil is characterized by high zoomass of Lumbricidae (dominant in terms of biomass are *Lumbricus terrestris* LINNAEUS, 1758, *Aporrectodea caliginosa* (SAVIGNY, 1826), *Octolasion* spp. [JUDAS, 1989]), Gastropoda (dominants are *Perforatella incarnata* (O. F. MÜLLER, 1774), *Arianta arbustorum* (LINNAEUS, 1758), *Aegopinella nitidula* (DRAPARNAUD, 1805), *Arion ater rufus* (LINNAEUS, 1758) [CORSMANN, 1981]), Diplopoda (dominants are *Glomeris marginata* (VILLERS, 1789), *G. conspersa* C. L. KOCH, 1847 [SPRENGEL, 1986], and Isopoda (dominant is *Trichoniscus pusillus* BRANDT, 1883 [STRÜVE-KUSENBERG, 1987]). In SO only a few slug species, with negligible population density, and no snail species occur. In the moder soil the earthworms are represented by the epigeic *Dendrobaena octaedra* (SAVIGNY, 1826) and other species near tree stumps (e.g. *Lumbricus rubellus* HOFFMEISTER, 1843); here mean body size of lumbricids is 8.8 mg dry mass, in comparison to 52.2 mg dry mass of the GÖ population.

Larvae of elaterid beetles are typical moder-soil inhabitants, consisting in SO almost solely of *Athous subfuscus* (O. F. MÜLLER, 1764). The community in GÖ is more diverse, with *A. subfuscus*, *A. vittatus* (FABRICIUS, 1792) and *A. haemorrhoidalis* (FABRICIUS, 1801) as the dominant species (MORITZ, 1986). In SO population density and biomass of dipteran larvae are considerably higher than in the mull soil of GÖ. Mean average individual mass of the larvae in GÖ is 0.057 mg dry mass, and in SO, 0.085 mg dry mass. Dominant families in GÖ (in terms of biomass) are Sciaridae, Empididae, Rhagionidae, Lestremiidae, Limoniidae and Tipulidae (HÖVEMEYER, 1984, 1985). In SO Sciaridae and Sciophilidae attain distinctly higher zoomass values than other dipterans (ALTMÜLLER, 1979).

Zoophagous macrofauna: The humus type has no dramatic effect on the colonization of the litter and upper soil layer by predatory macroarthropods. The moder soil is preferred by Araneida

and staphylinid beetles. In contrast, the mull environment in GÖ favours Pseudoscorpionida, Opilionida, Chilopoda and carabid beetles. Species numbers do not differ very much between SO and GÖ. However, it appears that the SO wood contains only few dominating species in every group, while the GÖ forest is characterized by more species of comparable numbers. The most prevalent species are: Araneida – in GÖ *Saloca diceros* (O.P.–CAMBRIDGE, 1871), *Micrargus herbigradus* (BLACKWALL, 1854), *Lepthyphantes zimmermanni* BERTKAU, 1890, *Walckenaera cuspidata* (BLACKWALL 1833), *Histopona torpida* (C. L. KOCH 1834) [STIPPICH, 1986]; – in SO *Coelotes terrestris* (WIDER, 1834) (about one half of total spider biomass), *Drapetisca socialis* (SUNDEVALL, 1832), *Tapinocyba pallens* (O. P. CAMBRIDGE, 1872) [ALBERT, 1982]. Pseudoscorpionida – *Neobisium muscorum* LEACH, 1817 in SO and GÖ, Opilionida – *Lophopilio palpinalis* (HERBST, 1799) and *Mitopus morio* (FABRICIUS, 1799) in GÖ and SO. Chilopoda – in GÖ, *Lithobius mutabilis* L. KOCH, 1862, *Strigamia acuminata* (LEACH, 1814), *L. piceus* L. KOCH, 1962 *Geophilus proximus* C. L. KOCH, 1847, *L. crassipes* L. KOCH, 1862 [POSER, 1984]; in SO, only *Lithobius mutabilis* and *L. curtipes* C. L. KOCH, 1847 [ALBERT, 1979]. Carabidae – in GÖ, *Abrax parallelepipedus* (PILLER & MITTERPACHER, 1783), *Carabus nemoralis* O. F. MÜLLER, 1764, *Pterostichus metallicus* (FABRICIUS, 1792) [MARTIUS, 1986]; in SO, *Pt. oblongopunctatus* (FABRICIUS, 1787). Staphylinidae – in GÖ, *Othius punctulatus* (GOEZE, 1777), *Philonthus fuscipennis* (MANNERHEIM, 1830), *O. myrmecophilus* KIESENWETTER, 1843, *Ph. rotundicollis* (MÉNÉTRIÉS, 1832), *Ph. decorus* (GRAVENHORST, 1802); in SO, only the two *Othius* species.

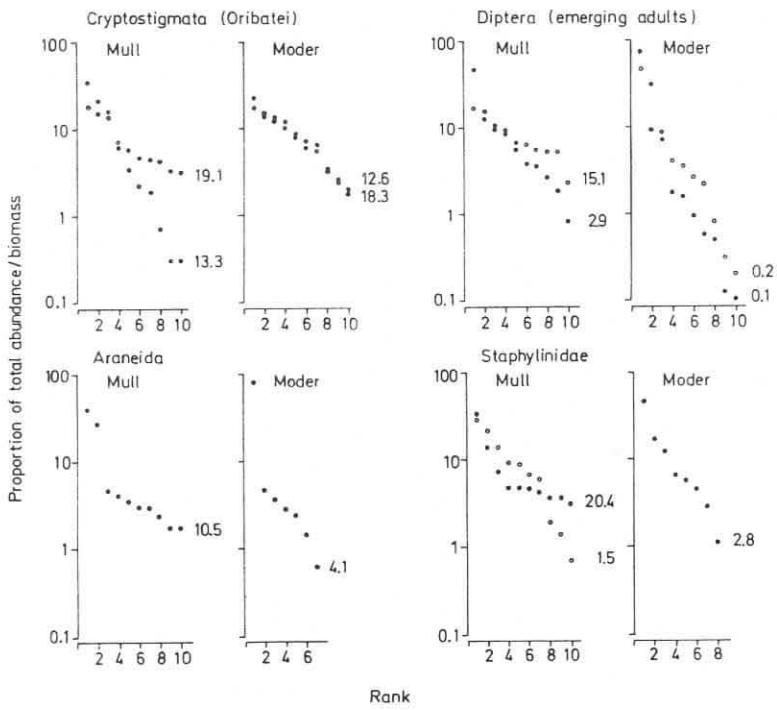

Fig. 1. Rank-abundance relation in a mull (Göttinger Wald) and a moder soil (Solling). (a) Cryptostigmata, annual catch of adults in 1981/82 (mull) (BAASKE, pers. comm.), 1987 (moder) (HEILIGENSTADT, 1988); (b) Diptera, emerging adults in 1981/82 (mull) (HÖVEMEYER, 1985), in 1973 (moder) (ALTMÜLLER, 1979); (c) Araneida, adults for 1981/82 (mull) (STIPPICH, 1981), for 1974/75 (moder) (ALBERT, 1982); (d) Staphylinidae, adults for 1980 (mull) (SCHAEFER, 1983), for 1974 (moder) (HARTMANN, 1979). Solid circles – abundance, open circles – biomass. Numbers behind the lines indicate the residual percentage value.

3.2. Species-abundance patterns and diversity

The number of species in many soil fauna groups are lower in SO than in GÖ (*cf.* table 1). The last paragraph contains examples of the dominance of one or two species in SO in contrast to a more even dominance-diversity relation in GÖ. A more detailed analysis of soil fauna types reveals a more complex situation; regrettably, for some animal groups of the moder soil no detailed data are available.

For oribatid mites (as **saprophagous and microphytophagous mesofauna**), rank-abundance relation in the moder litter-soil environment is more balanced than in the mull situation (fig. 1). This does not apply to enchytraeid worms. There are indications that the Collembola display a similar pattern as the Oribatida.

Diversity values of the **saprophagous macrofauna** are high in the mull forest. This is also true for the larval populations of Diptera (*cf.* fig. 1).

For the **Zoophagous macrofauna,** differences between mull and moder are not very striking. However, diversity values tend to be higher in the mull soil-litter subsystem (*cf.* fig. 1).

3.3. Vertical distribution

The moder populations tend to be confined to the organic layers of the soil, whereas the mull environment favours populations which penetrate deeper into the soil (fig. 2). Two factors contribute to this tendency: avoidance of the litter layer and/or preference of deeper soil layer.

This tendency even applies to the semiaquatic **microfauna**. In SO the testate amoebae mainly occur in the O_f layer (MEISTERFELD, 1980), while in GÖ testate amoebae, naked amoeba and flagellates tend to be confined to the soil (MEISTERFELD, 1989).

For all groups of the **saprophagous and microphytophagous mesofauna**, mean depth values of GÖ are distinctly lower than in SO (*cf.* fig. 2). The same tendency can be observed for the Gamasina as a **zoophagous mesofauna** group.

Saprophagous macrofauna: The litter layer of SO is the stratum preferred by *Dendrobaena octaedra* as an epigeic lumbricid. More than 50% of the larvae of the elaterid beetle *Athous subfuscus* occur in the L and O_f horizons of SO (MORITZ, 1986). Dipterous larvae of SO clearly prefer the organic strata (*cf.* fig 2). In contrast, among the mull macrofauna of GÖ, Elateridae,

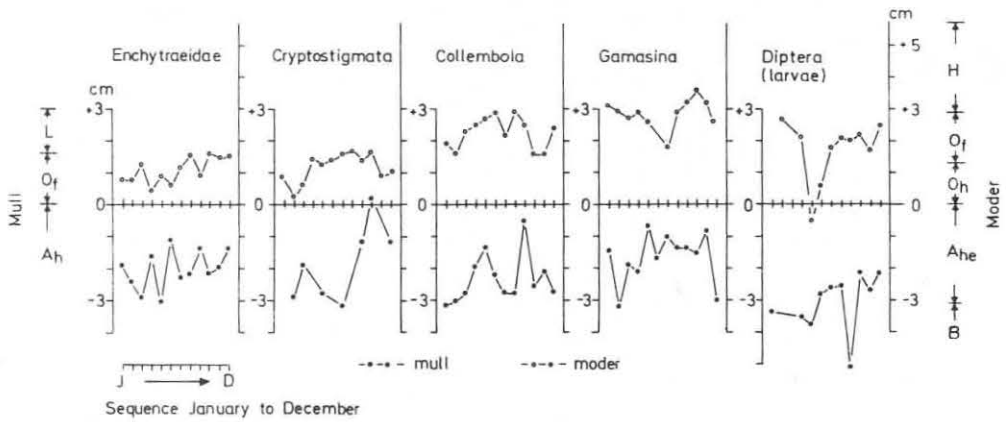

Fig. 2. Vertical distribution of Enchytraeidae, Cryptostigmata, Collembola, Gamasina and larvae of Diptera in a beech wood on mull soil (Göttinger Wald) and on moder soil (Solling). Mean depth values are calculated from abundance data given by WOLTERS (1983) (Collembola, mull), HÖVEMEYER (1984) (dipterous larvae, mull), ELLENBERG et al. (1986) (Enchytraeidae, Collembola, Diptera in moder soil), SCHULZ (1986) (Gamasina, mull), MELLIN (1988) (Enchytraeidae, mull), HEILIGENSTADT (1988) (Cryptostigmata, moder), BAASKE (pers. comm.) (Cryptostigmata, mull), HEILIGENSTADT (pers. comm.) (Gamasina, moder). Calculations for dipterous larvae in the moder soil are based on % samples which contain dipterans. For further details *cf.* "Methods".

Diptera and Lumbricidae reach deeper into the soil. For instance, endogeic earthworms living in the mineral soil constitute over 40 % of lumbricid zoomass in comparison to 50 % of the anecic species *Lumbricus terrestris* and 4 % epigeic litter-dwelling forms (JUDAS, *et al.* 1989).

In both habitats, most species of the **zoophagous macrofauna** are confined to the litter environment (*cf.* fig. 2). The chilopods are an exception, with about half of the individuals (mainly Geophilomorpha) in the deeper mineral strata (POSER; 1984).

3.4. Phenology

No clear picture emerges in the sequence of phenological events in both habitats, measured as changes of biomass throughout the year. In the moder soil the mesofaunal groups tend to fluctuate more widely. Generally, however, the fauna appears to be more continuously present in SO, whereas the mull soil in GÖ is characterized by a sequence of different phenophases: winter depression in the "active" biomass of the macrofauna, high activity and population density in spring and autumn, minimum of faunal development in some groups during summer with conditions of low soil moisture (fig. 3).

3.5. Trophic organization

A calculation of the relative proportion of trophic types in faunal biomass (partly only as a rough estimate; see SCHAEFER, 1990) leads to the following results (table 2): in SO macrohumiphages are far less important than in GÖ, on the other hand, microphytophages (fungal feeders)

Table 2. Representation of trophic types among the mesofauna and macrofauna in the mull (Göttinger Wald) and moder soil (Solling).

Trophic type	Mean annual biomass (mg dry mass · m^{-2})	
	Mull	Moder
Saprophages		
Macrohumiphages[a])	6817	1375
Microhumiphages[b])	5842	1452
Microphytophages		
Mycophages[c])	340	662
Bacteriophages	+	+
Phycophages	+	+
Macromycophages	+	+
Rhizophages	+	+
Zoophages		
Microzoophages, mesozoophages[d])	45	397
Macrozoophages[e])	513	711

[a]) Enchytraeidae 50 %, Gastropoda 100 %, Lumbricidae 50 %, Isopoda 50 %, Diplopoda 100 %, Diptera 45 % in mull, 75 % in moder; [b]) Enchytraeidae 25 %, Cryptostigmata and Collembola 50 %, Lumbricidae 50 %, Isopoda 25 %, elaterid larvae 100 %, Diptera 30 % in mull, 5 % in moder; [c]) Enchytraeidae 25 %, Cryptostigmata and Collembola 50 %, Isopoda 25 %, Diptera 5 % in moder; [d]) Gamasina 100 %; [e]) Diptera 15 %, Araneida 100 %, Pseudoscorpionida 100 %, Opilionida 100 %, Chilopoda 100 %, Carabidae 100 %, Staphylinidae 100 %. Note: Because of the incomplete faunal survey only absolute biomass values are given. These – rough – estimates are calculated from trophic classifications of the group in question (PERSSON *et al.*, 1980; ELLENBERG *et al.*, 1986; SCHAEFER, 1990) and mean annual biomass (*cf.* Table 1). Detailed food analysis is based upon MELLIN (1988) for Enchytraeidae, JUDAS (1989) for Lumbricidae, STRÜVE-KUSENBERG (1987) for Isopoda, MORITZ (1986) for elaterid larvae, HÖVEMEYER (1985) for mull Diptera, ALTMÜLLER (1979) for moder Diptera. Accessory food preferences could not be taken into account. Only groups with biomass values for the moder and the mull soil are included. + = no quantification given.

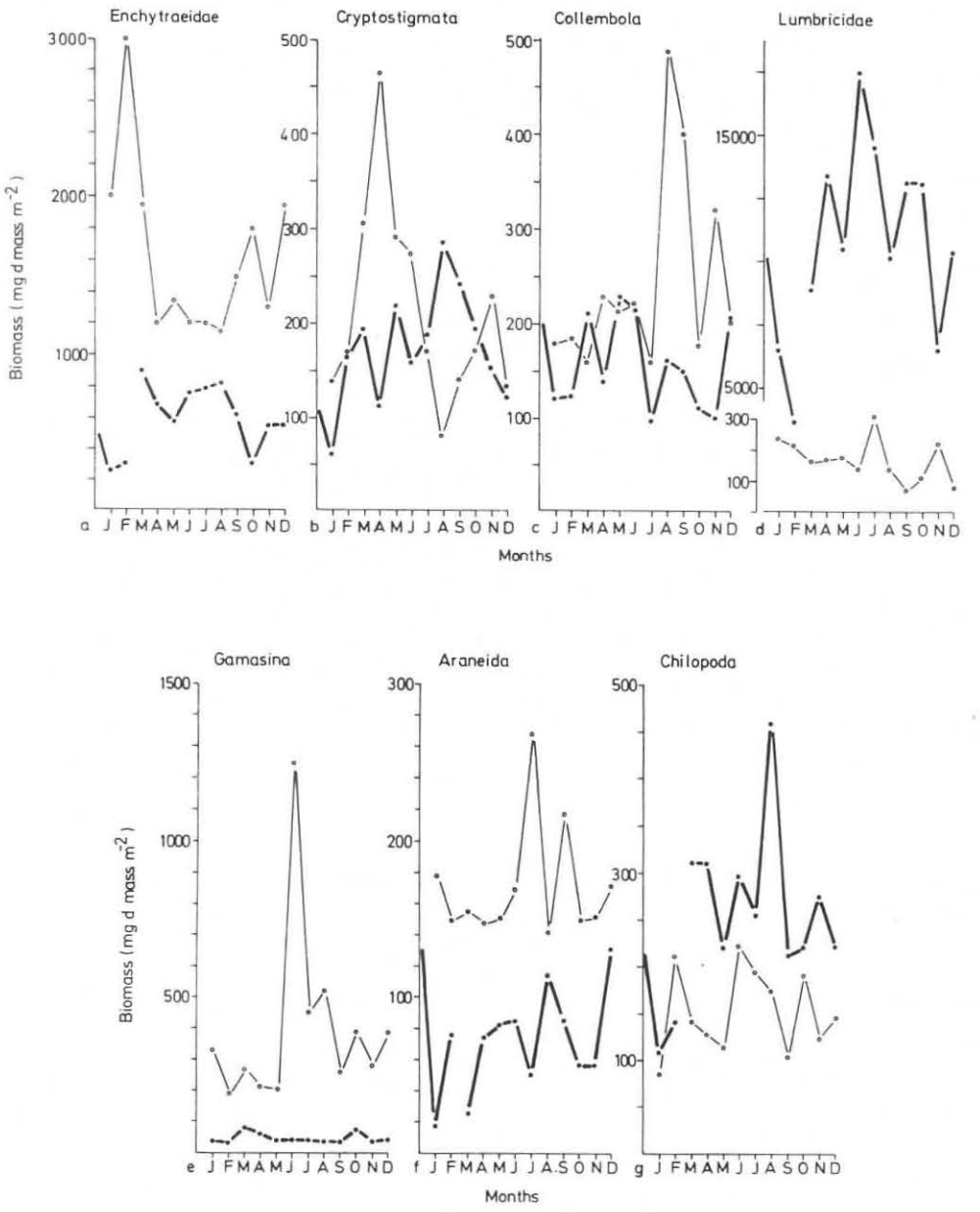

Fig. 3. Phenology (as biomass; mg dry mass · m^{-2}) of soil animal groups (Enchytraeidae, Cryptostigmata, Collembola, Lumbricidae, Gamasina, Araneida, Chilopoda) in a beech wood on mull soil (Göttinger Wald) and on moder soil (Solling). Thick line – GÖ, thin line – SO. Data for the animals groups in moder soil from ELLENBERG et al. (1986), for Enchytraeidae (mull) from MELLIN (1988), for Cryptostigmata (mull) from BAASKE (pers. comm.), for Collembola (mull) from WOLTERS (1983), for Lumbricidae (mull) from JUDAS (1989), for Gamasina (mull) from SCHULZ (1986), for Araneida (mull) from STIPPICH (1986), for Chilopoda (mull) from POSER (1984).

dominate in the moder soil. Mesopredators (Gamasina) are well developed in SO. Macropredators have a comparable zoomass in both forests.

4. Discussion

4.1. General pattern of species, abundance and biomass for mull and moder soils

Are the mull-moder differences between GÖ-SO in accordance with conditions in other European forests? PETERSEN & LUXTON (1982) and SCHAEFER (1989c) summarize the characteristics of the soil fauna in mull and mor soils of temperate deciduous forests. An estimate of total faunal biomass for Meerdink (Netherlands) with moder soil is 5.2 g dry mass m^{-2}. Biomass estimates for the soil fauna of mull soils range from 8 g dry mass m^{-2} (Hestehave beech forest, Denmark) to a value of about 30 g dry · mass m^{-2} for a hornbeam *(Carpinus betulus* L.) forest at Brunoy (France). Generally, in temperate climates maximum faunal biomass is found in deciduous woodlands and grasslands on base-rich soils. Thus mull soils are characterized by much higher total soil fauna biomass than moder and mor soils. Mull soils are dominated by Lumbricidae, snails and slugs, isopods, diplopods. These taxa are poorly represented in deciduous forests on moder soils. Mor and moder soils are inhabited by larger numbers of Enchytraeidae, oribatid mites, collembolans and dipterans.

Earthworms emerge as a soil fauna "key group". PETERSEN & LUXTON (1982) state that fertile mull soils of the temperate region have higher numbers of earthworms, with a high proportion of large anecic and endogeic species. On the other hand, moder or mor soils, with insignificant earthworm populations, have small epigeic species, e.g. the acid tolerant *Dendrobaena octaedra, Lumbricus rubellus* or *Dendrodrilus rubidus* (SAVIGNY, 1826) [WALLWORK, 1976]. The data show clearly the generally higher earthworm biomasses in soils without the organic top horizon, including the typical mull soils of temperate forests. This distinction between earthworm populations in mull and mor (or moder) forest soils was also found by PHILLIPSON *et al.* (1978).

Thus the differences between mull and moder in GÖ and SO are in accordance with the general pattern that has emerged from characterizing other mull and moder forests.

The data presently available for forest ecosystems suggest an inverse relationship between mass of accumulated organic material on the soil surface and the total soil fauna biomass (O'NEILL & REICHLE, 1979), which tentatively has been approximated by a negative power function (PETERSEN & LUXTON, 1982). The input rate of litter as the primary nutrient source for the decomposer food web does not seem to be the most significant factor determining the biomass of the soil fauna.

Factors being responsible for the difference in the faunal component of the litter-soil subsystem in mull and moder soils might be: temperature, soil *p*H, base saturation, soil moisture, quality of food (microflora, herb litter), and the degree of stability or disturbance of soil stratification. Some suggestions about the different habitat preferences of the fauna are possible. Probably Protozoa and Nematoda utilize the rich bacterial populations in mull soil, and microfaunal populations feeding on fluids depend on rapid nutrient turnover. The reason for the suppression of shell-bearing gastropods appears to the low Ca availability. This element is a prerequisite for the formation of the shell. Enchytraeids need high moisture (PETERSEN & LUXTON, 1982), which is secured more in moder or mor soils than in mull soils. Population density and biomass of Enchytraeidae are inversely related to population density and biomass of earthworms and perhaps are directly influenced by earthworms. The susceptibility of individuals to low *p*H values (PIEARCE, 1972; EDWARDS & LOFTY, 1977) may be one reason for the absence of most earthworm species in acid soils. Furthermore, the habit of substrate feeding is not possible in the A horizon of moder and mor soils. Many oribatid mites and collembolans are preferably fungal feeders and may be favoured by high population densities of microfungi in moder or mor soils. The reason for the absence of isopods and diplopods in acidic moder and mor soils may be the low Ca availability, this element being an important constituent of the exoskeleton. The

voluminous topsoil organic layers in the moder and mor ground floor may favour the establishment of predatory macrofauna populations, such as spiders, carabids and staphylinids (SCHAEFER, 1983). The chilopods that penetrate deeper into the soil (mainly Geophilomorpha) appear to be favoured by the crumb structure of the A_h horizon in the GÖ mull soil, which is additionally aerated by the activity of earthworms. The availability of lumbricid worms as food may also favour chilopod populations. According to WALLWORK (1976), zoophagous arthropods (such as gamasid mites, centipedes, spiders, pseudoscorpions, opilionids, and predatory beetles) are generally better represented in moder profiles than in mull, probably parallel to the higher numbers of microarthropods as prey.

4.2. Species-abundance patterns and diversity

A general outcome of the study is the fact that values of diversity tend to be higher in the mull forest GÖ than in the moder soil of SO. Notable exceptions might be some microphytophagous and zoophagous animal groups. The trend to higher species numbers and to less extreme dominance patterns is also found in arthropod groups that were not studied in the present paper. Species numbers for GÖ and SO, respectively, are the following: Coeloptera 254 and 225; curculionid beetles 34 and 12; Lepidoptera 53 and 40 (WINTER, 1985; ELLENBERG *et al.*, 1986; WAGNER & SCHAEFER, 1989). ULRICH (1989) estimates species of Hymenoptera in GÖ to approach 1,000.

Decisive factors for higher species numbers and values of diversity in the mull environment can be many. The two main influences are (1) the more variable spatial environment resulting from the herb stratum and the effects of the macrofauna (mainly earthworms) on soil properties; and (2) presence of a wider variety of herbaceous and microfloral (at least bacterial) food resources. This leads to a mosaic structure of the habitat in horizontal and vertical directions, which facilitates the coexistence of many species (SCHAEFER, in prep.).

In the moder environment the structurally diverse litter layer and the presence of high numbers of fungal populations may favour microphytophages and some litter-dwelling predatory arthropods.

4.3. Vertical distribution

In the moder soil of SO most of the animal populations are concentrated in the comparatively thin organic layer ($L + O_f + O_h + A_h$). In contrast, the GÖ populations penetrate deeper into the soil, the A_h horizon being much more extensive in the mull than in the moder soil. Deep burrowing and endogeic earthworms contribute to mixing of organic and inorganic material (bioturbation), thus providing organic matter as food resources for saprophagous and/or microphytophagous animals in deeper strata of the soil. Litter-feeding earthworms in acidic soil environments utilize the pronounced availability of Ca in the litter layer. Substrate-feeding species are favoured in mull soils by the presence of the A_h horizon rich in organic material. Of course, this vertical distribution pattern of the soil animals is modified by seasonal and diurnal migrations, which can be decisive for the "functional" stratification of the fauna in relation to soil factors and resources.

4.4. Phenology

It is difficult to detect differences in seasonality between the soil and litter animal populations in mull and mor forest floors. In GÖ the soil normally becomes rather dry during summer, particularly in July and August, which may lead to a phase of inactivity or low population numbers of certain animal groups. High abundances of the soil fauna in winter are typical for SO, as compared to GÖ, where some populations significantly decrease, probably because freezing of the soil may occur in mull profiles causing vertical migrations and/or increased rates of mortality.

Subzero temperatures rarely occur in moder or mor profiles, because the thick organic topsoil serves as an insulation layer during periods without snow.

Another complex of factors contributing to the stronger seasonality of soil and litter animals in GÖ may be the variance of food resources, mainly originating from the input of organic matter from above-ground and below-ground herb biomass.

4.5. Trophic organization

The main difference between GÖ and SO is the preponderance of the macrohumiphagous macrofauna in the mull soil and the mycophagous mesofauna groups in the moder soil. The importance of mycetophages is easily explained by the fact that in SO fungi account for more of the microbial biomass: the relation between bacterial and fungal biomass was 37:63 in the O_h layer and 30:70 in the O_f layer (ELLENBERG *et al.*, 1986). In the soil of GÖ the mean proportion of bacterial biomass was 45% (DOMSCH & VANSELOW, pers. comm.). In accordance with this result, WALLWORK (1976) found indications that moder and mor soil generally contain more mycetophages, and in particular more fungal feeders among collemboles and oribatid mites, than mull soils.

In mor and moder soils leaf litter and partly decomposed litter are more abundant resources than in mull soils. It is astonishing that the fauna in moder soils appears not to be better adapted to utilizing these food resources. The gap left by the absence of the comminuting macrofauna has not been closed by members of the mesofauna such as enchytraeids, collembolans, mites or the dipterous larvae. One important point may be that high-quality litter is not offered in the moder ground zone, whereas the occasional presence of herb litter in the mull forest facilitates the consumption of low-quality beech litter.

It should be emphasized that the comminuting effect of the saprophagous macrofauna in the mull soil leads to translocation of organic material onto and into the mineral soil (SCHAEFER, 1989a), while communition of litter in the moder system is confined to the organic topsoil.

4.6. Decomposition in mull and mor soils

The decomposition rate k as the ratio of the annual input of canopy leaf litter to the mean annual standing crop of canopy leaf litter is about 0.25 in SO (approximate value calculated from the quotient leaf litter fall/litter standing crop according to ELLENBERG *et al.*, 1986); in GÖ k has a value between 0.6 and 0.8 (JÖRGENSEN, 1987; SCHAEFER, 1990). HERLITZIUS & HERLITZIUS (1977) found significant differences for the decay of beech leaf litter in SO and GÖ. Decomposition rates (including comminution and tranlocation into the soil) are generally higher in mull than in moder or mor forest soils (SWIFT *et al.*, 1979), contributing to lower standing crop of soil organic matter in the first soil type.

The reason for the different decay rates in these soil types is complex. However, it can be related to the different composition of soil fauna. Higher rates in mull soils are the result of litter comminution by the macrofauna, mixing of organic material with the mineral soil and the maintenance of well-drained aerobic conditions in the soil. Moder soil, on the other hand, has low *p*H values in all strata (produced by acid litter or acid soil parent material) that inhibit the macrofauna and prevent its feeding and burrowing activities (SWIFT *et al.*, 1979). Additionally, decomposition may be inhibited in moder and mor soil by the presence of phenolic acids in litter, by the water-holding capacity of organic material and higher grazing pressure on fungal decomposers (DICKINSON & PUGH, 1974; SWIFT *et al.*, 1979). As a general rule faunal biomass is positively correlated with decomposition rate.

4.7. Importance of animals in energy flow

For both forests detailed energy budgets have been calculated. In SO soil animals are reponsible for about 12% of soil heterotrophic respiration. When the ingestion rates of all saprophagous and microphytophagous animals are summed up, a high amount of organic material is consumed, corresponding to a high percentage of the energy content of annual leaf litter input (GRIMM & FUNKE in ELLENBERG *et al.*, 1986). In GÖ the animal component of total soil respiration surpasses 10%. In terms of energy units, almost the whole amount of aboveground leaf litter input is consumed by "saprophagous" animals, in this case mainly by the litter comminuting macrofauna (SCHAEFER, 1989d, 1990). Obviously in terms of energy flow, the moder soil fauna, with a significantly lower biomass, is as important as the mull fauna, a result which probably cannot be generalized (PETERSEN & LUXTON, 1982). In this connection it should be mentioned that mean body size of the moder fauna is distinctly lower than that of the mull fauna, contributing to higher metabolic rates. Additionally, the calculation of global energy budgets can yield only rough estimates. However, the striking difference is that a high proportion of animal carbon metabolism in the mull forest is due to primary consumers of litter, whereas in the moder soil secondary consumers – detritus and microflora feeders – contribute more to soil fauna metabolism.

4.8. Patterns of mineralization and nutrient release

By interaction with the microflora, soil animals serve as driving variables for microfloral activity, which can be related to decomposition and mineralisation events. From a number of studies the following tentative conclusions can be drawn (SCHEU, 1987a, 1987b; WOLTERS, 1988, 1989): Under mull conditions animals tend to increase microbial activity; in the moder environment microbial-determined rates of matter transfer tend to be depressed by grazing mesofaunal populations.

In GÖ carbon mineralisation rates – measured as soil respiration – and nitrogen net mineralisation rates are high from May to September, with some irregular depressions (REICHARDT, 1982; ANDRES, 1984). In contrast, in the layers O_f and O_h of the SO moder soil, carbon mineralisation has a distinct peak in September; nitrogen mineralisation rates, determined for the O_h and A_{he} layers, have maxima in spring and autumn (ELLENBERG *et al.*, 1986).

It is difficult to correlate the pattern of the annual cycle of carbon and nitrogen mineralization with animal population data. However, the permanent presence of high zoomass during the vegetation period in the mull forest contributes to continuity of bioelement dynamics, while the fauna of the moder soil – confined to the upper strata of the soil-litter subsystem – cannot compensate for negative influences of abiotic factors, such as periods of low topsoil moisture – on microbial activity.

4.9. Conclusion: general characteristics of mull and moder soil subsystems

The 7 hypotheses formulated above have been verified by our study. The moder soil is correlated with lower faunal biomass, with low representation of macrofauna and high abundance of mesofauna, with low species diversity, with concentration of animals in the organic layer, with no sharply defined phenophases, with utilization of a few types of food resources, with minor importance of animals in determining decomposition and no clearcut positive influence of the fauna on mineralization. Conversely, the mull soil with a higher zoomass is macrofauna-dominated, has a high species diversity, is inhabited by animals in deeper soil layers, is characterized by more distinct phenophases, is inhabited by a fauna utilizing a diversity of food recources, is dominated by animals as driving variables for microbial activity, and is characterized by a more continous pattern of carbon and nitrogen metabolism during the vegetation period.

However, causal relationships are far from clear. A "key factor" are the abundance and activity of the macrofauna, which in turn determines the pattern of material flow in the litter-soil

subsystem. Are many macrofaunal groups suppressed in the moder environment by direct effects of low *p*H, by low cation availability, by lower quality of leaf litter, by factors correlating with the thick and dense organic layer or by other, still unknown influences? This indicates future essential lines of study in order to understand the sequence of effects between structural and functional properties of the system leading to distinct differences in ecosystem processes.

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The soil fauna of a mull beech forest on limestone (Göttinger Wald) in southern Lower Saxony is compared to the soil fauna of a nearby moder beech forest on red sandstone (Solling). In comparison to moder conditions, the mull forest is characterized by higher species numbers, more equable rank-abundance relations, higher faunal biomass (approximately 15 g dry mass $\cdot m^{-2}$), dominance of macrofauna and microfauna, and greater trophic diversity with a preponderance of saprophagous animals. In contrast, the moder forest has lower species numbers with only few species dominating, lower faunal biomass (about 5 g dry mass $\cdot m^{-2}$), and higher numbers of mesofaunal, microphytophagous animals. The mull soil fauna penetrates to deeper soil horizons than the moder soil fauna. Under moder soil conditions the biomass of the mesofauna tends to fluctuate widely. In terms of energy flow, the soil animal community is of similar importance in both humus types. However, the predominance of macrofauna in the mull system contributes to higher decomposition rates. It is hypothesized that moder soil biota are more sensitive to stress factors, a situation which leads to a more seasonal pattern of carbon and nitrogen mineralisation.

Key words: Soil fauna, beech forest, mull, moder, biomass, diversity, trophic organization.

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